Submodels of Apple Snail Model

Environmental conditions

We assume a grid of 400 x 400 meter cells covering the area of the Everglades Depth Estimation Network (EDEN). For each cell, we assume that we can assign:

- a discrete habitat class (according to the fraction of usable habitat in the cell)
- daily values of water depth
- daily values of ambient air temperature.

Daily empirical time series data over multiple years on water stage from gaging stations can be input to the model. Temperature data may be available from the USDA. Habitat classes can be determined from vegetation maps.

Population

The size structured apple snail population is represented as a vector consisting of 600 age-classes;

$$\mathbf{N} = [N_1(t), N_2(t), \ldots, N_i(t), \ldots, N_{600}(t)] \tag{1}$$

where t is time and i is age in days.

Growth

A logistic function is used to describe the size, $Size_i$ of all individuals within a given snail cohort of age i;

$$Size_i = \frac{Size_{min} e^{k_{growth} Age}}{1 + (Size_{min} / Size_{max})(e^{k_{growth} Age} - 1)} \tag{2}$$

$Size_{min}$ = Size of newly hatched snail

$Size_{max}$ = Maximum size of snail

k_{growth} = Daily growth rate

Parameter estimates are listed in Table A1.

Survival

Here we determine the values of day-to-day survival, $a_{i,i+1}$, which depend on age and size.

Survival during conditions of flooding (water depth > 0 cm)

$surv_{1,wet}$ = survival for snails $Size_i \leq 6$ mm

$surv_{2,wet}$ = survival for snail 6 mm $\leq Size_i <$ 10 mm

$surv_{3,wet}$ = survival for snails 10 mm $\leq Size_i <$ 16 mm

$surv_{max,adult,wet}$ = coefficient survival for snails 16 mm $\leq Size_i$

Although the model has an array of 600 cohorts, the life of adults does not extend much beyond 500 days. In order to achieve rapid die off around this age, we substitute the following expression for survival of snails of size > 16 mm.

$$Surv_{adult,wet} = \frac{surv_{maxadult,wet}}{1 + e^{-k_{age}(Agemort - Age)}} \tag{3}$$

where

Age = age of cohort in days

Age_{mort} = assumed mean upper age limit on snails

k_{age} = coefficient causing rapid die of at end of lifespan

Survival during dry conditions (water depth ≤ 0 cm).

$surv_{1,dry}$ = survival for snails $Size_i \leq 6$ mm

$surv_{2,dry}$ = survival for snail 6 mm $\leq Size_i <$ 10 mm

$surv_{3,dry}$ = survival for snails 10 mm $\leq Size_i <$ 16 mm

$surv_{4,max\ adult,dry}$ = survival for snails 16 mm $\leq Size_i$

As above, the life of adults does not extend much beyond 540 days. In order to achieve rapid die off around this age, we substitute the following expression for mortality of snails of size > 16 mm.

$$Surv_{adult,dry} = \frac{surv_{max\,adult,dry}}{1 + e^{-k_{age}(Age_{mort} - Age)}} \qquad (4)$$

The parameters $surv_{max\ adult,wet}$, $surv_{max\ adult,dry}$, Age_{mort} , and k_{age} can be adjusted by those using the model.

Reproduction

New 1-day old snails are given by

$$N_1\,(t+20) = f_i N_i\,(t) + f_{i+1} N_{i+1}(t) \ \ldots\ + \ldots f_{600}\, N_{600}(t) \qquad (5)$$

Here we determine the values of f_i, or the numbers of offspring produced per female snail per day. We can write f_i as a product of factors:

f_i = (*Female fraction*) x (*Fraction sexually mature*) x (*Clutch size*)

x (*f(time of year)*) x (*f(temperature)*) x (*f(water depth)*)

We consider each of these factors in turn.

Female fraction = fraction of snails of age i that are female

Fraction sexually mature = fraction of females of age that is sexually mature

This will depend on size, which we calculated earlier. We assume that there is a mean size of arrival at maturity, or

$Size_{maturity}$ = mean size at which snail is assumed to be mature,

but there is some variation about this value, expressed as a cumulative fraction of reproductive females

$$Cumulative\ fraction\ of\ mature\ females\ at\ age\ i = \frac{e^{k_{repr}(Size_i - Size_{maturity})}}{1 + e^{k_{repr}(Size_i - Size_{maturity})}}, \qquad (6)$$

where

$Size_i$ = the size of females in age class i

k_{repr} = coefficient describing rate at which females enter reproduction as a function of age close to mean size at maturity. This will result in virtually all females being sexually mature by Size = 30 mm.

Clutch size = size of clutch laid by a single female snail

f(time of year) = effects on reproduction of time of year

f(water depth) = effects on reproduction of water depth

f(temperature) = effects on reproduction of temperature

The probability of reproduction decreases rapidly as temperature decreases below 17° Celsius. We can represent this as,

$$f(temperature) = \frac{1}{1 + e^{-k_{temp}(temperature - teperature_{reprod})}}, \qquad (7)$$

where

$temperature_{reprod}$ = temperature below which reproduction rate decreases rapidly

k_{temp} = coefficient for temperature effect on reproduction

We also impose an upper limit on the number of eggs. There should be some upper limit, because of the limited number of emergent macrophytes on which to deposit eggs. We do not know what this limit is, and it will vary from cell to cell. We only can make an estimate.

Egg limit = carrying capacity of a spatial cell for eggs

If this limit is reached, no more eggs are assumed oviposited. It is possible that it will not be necessary to impose such an upper limit.

Egg survival under submerged conditions

If water level rises more than 18 cm after eggs have been laid, then those eggs will likely be submerged and mortality can occur. It is assumed that eggs submerged for 14 or more days will suffer 95% mortality. To compute this egg mortality, the computer code stores the numbers of eggs laid and water levels on each of the preceding 20 days. If water level rises on the current day is 18 cm higher than the water level on any of the preceding 20 days, then the day-cohort of eggs on that day is followed to see if it remains flooded for 14 or more days. As soon as that criterion is reached, the number of eggs in that day cohort is reduced by 95%.

Table 1. Parameter values used in the Apple Snail model

Parameter	Value
$Size_{min}$	3 mm
$Size_{max}$	50 mm
k_{growth}	0.05 day^{-1}
$surv_{1,wet}$	1.0 - 0.013 day^{-1}
$surv_{2,wet}$	1.0 - 0.013 day^{-1}
$surv_{3,wet}$	1.0 - 0.013 day^{-1}
$surv_{max\ adult,wet}$	1.0 – 0.01 day^{-1}
$surv_{1,dry}$	1.0 - 0.024 day^{-1}
$surv_{2,dry}$	1.0 - 0.016 day^{-1}
$surv_{3,dry}$	1.0 - 0.011 day^{-1}

$surv_{max\ adult,dry}$	1.0 - 0.01 day^{-1}
Age_{mort}	500.
k_{age}	0.1
$Size_{maturity}$	27.5 mm
Female fraction	0.5
k_{repr}	1.0
Clutch	30 eggs
$temperature_{reprod}$	17° C
k_{temp}	1.0
f(time of year)	1.0 January 15 $\leq$ *time of year* < April 1
f(time of year)	1.0 April 1 $\leq$ *time of year* < July 1
f(time of year)	0.3 July 1 $\leq$ *time of year* < November 15
f(time of year)	0.0 November 15 $\leq$ *time of year* < January 15
f(water depth)	0.0 *water depth* < 10 cm
f(water depth)	$1.0 - (water\ depth - 50\ cm)^2 / 40^2$ 10 cm $\leq$ *water depth* < 90 cm
f(water depth)	0.0 90 $\leq$ *water depth*
Egg limit	35,000 ha^{-1}